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Bacteria on the food, in the intestine and on the faeces of the woodlouse *Oniscus asellus* (Crustacea, Isopoda)

Species composition and nutritive value

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With 12 figures

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1. Introduction

The role of bacteria in the life of arthropods feeding on cellulose-rich diets is a well investigated topic. The benefit of the activities carried out by bacterial symbionts in termites (Isoptera) has been treated by many authors (i.e. Breznak, 1982). Detailed information also exists concerning the composition of the gut microflora in the cockroach *Periplaneta americana* [Cruden & Markovetz, 1987].

In contrast to all other arthropods, the gut of woodlice is simply a straight tube lined by a cuticle. The environmental conditions in the woodlouse gut are thus quite different from those in cockroaches or termites. A strategy similar to these insects, whose auxiliant symbiotic bacteria show a constant association with the host's gut and live only under partly anaerobic conditions, seems not to be verified in woodlice. References to the existence of possible symbionts in woodlice as permanent inhabitants of the intestinal tract (Carefoot, 1984a, Carefoot, 1984b; Carefoot, 1989; Wood & Griffiths, 1988) are indirect or do not differentiate between forms ingested with the food and the indigenous microflora of the intestinal tract.

For *Oniscus asellus* L. a special way of exploiting the natural food seems necessary. One possibility of enhancing this process through the use of the various abilities of microorganisms may be coprophagy.

Little is known about the change in bacterial species composition from leaf litter to faeces while passing the intestinal tract. Contradictory statements dealing with the gut flora of woodlice are based on the use of unstarved animals, whose gut microbiota mainly reflect the heterogeneous environmental bacteria ingested with the food.

By analyzing the bacterial microflora on leaves, in the intestine, and on the faeces, the selectivity of the intestinal tract of *Oniscus asellus* is documented. By testing the nutritive value of isolated faeces bacteria, their role in the phenomenon of coprophagy was assessed.

2. Materials and methods

2.1. Preparation of bacterial samples

For the isolation of litter inhabiting bacteria, partly decomposed leaves of *Acer pseudo-platanus L.*, *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Lieblein, which served as food for specimens of *Oniscus asellus*, were used. They were intensively ground, filled in glass tubes, and covered with a sterile 0.8% NaCl-solution. After vigourously shaking, aliquots of the supernatant fluid were streaked onto the surface of trypton-yeast-agar (trypton 10%, yeast extract 5%). This medium was adjusted to *p*H 7.0. The inoculated plates were incubated at 22°C.

The extraction of the intestine of *Oniscus asellus* was carried out on three adult specimens, which were kept for one month in plastic boxes (20 cm·20 cm·6 cm) at 14°C. The bottoms of the boxes were covered with

moistened plaster of Paris. The animals were starved for 12 days, so that strains of autochthonous intestinal bacteria or such forms being resistant to a longer gut stay were principally obtained.

For the extraction of the intestinal tract, the specimens were washed with 70% ethanol for a few seconds to prevent a contamination of the opened body cavity by bacteria from the rich exomicroflora adhering to the cuticle surface of *Oniscus asellus*. After washing them again with sterile distilled water, the animals were dissected in a petri dish filled with sterile 0.8% NaCl-solution. The intestine was removed with sterile tweezers and divided into stomach, midgut glands, and hindgut. After transferring the tissues into glass tubes, each of which contained 1 ml of physiological NaCl-solution, they were intensively crushed with a glass bar. The cloudy liquid was diluted and streaked out on trypton-yeast agar (*p*H 7.0) in portions of 0.2 ml. The petri dishes were incubated at 22°C.

The faeces inhabiting bacteria of *Oniscus asellus* were obtained by collecting the faecal pellets from specimens kept in plastic boxes. The faeces had an age of 2–3 weeks. At this state they were most preferred by *Oniscus asellus* [HASSALL & RUSHTON, 1985]. Five mg faeces (wet mass) were suspended in 5 ml bidistilled water and shaken on a vortex mixer. The clear supernatant fluid was serially diluted up to a dilution of 10^{-4}. Each 0.1 ml was parallely streaked out on trypton yeast agar (TYA) and used as an inoculum for a liquid TYA-medium.

A leaf agar was prepared to test the ability of faeces-bacteria grown on TYA to grow on a less rich medium.

Partially decomposed leaves from *Acer pseudoplatanus*, *Fagus sylvatica*, and *Quercus petraea* were homogenized. Portions of 10 g were added to 1000 ml distilled water with 1.5% agar. The *p*H was adjusted to 6.5. Both trypton yeast (petri dishes and liquid medium) and leaf agar were incubated at 22°C.

2.2. TEM-observations on bacteria

Two days old, pure cultures of isolated bacterial strains were used for TEM-investigations after negative staining.

The bacteria were taken from the agar-plates in small portions and suspended in bidistilled water on a glass slide. A small drop of the suspension was placed on a formvar coated 200 µm mesh size copper grid. After slight drying, the bacteria were coated either with 1% uranylacetate (*p*H 4.7) or 2% phosphor-tungsten acid (*p*H 7.0) for maximally 5 seconds. The dry grids were examined in a Zeiss EM 9 S-2.

2.3. Identification of bacteria

The isolated bacteria from litter, intestinal tract, and faeces were identified by 22 different diagnostic tests. "Bergey's Manual of Determinative Bacteriology" 8th edition (BUCHANAN & GIBBONS, 1974) and 9th edition volume I (KRIEG & HOLT, 1984) and volume II (SNEATH *et al.*, 1986) were used for the determination of the bacteria. Additionally, the medical API 20 E diagnostic tables for gram negative bacteria were used.

2.4. Feeding of *Oniscus asellus* with faeces-bacteria

To assess the nutritional role of faeces-bacteria eaten by woodlice via coprophagy, pure cultures of determined bacterial strains were offered to the test animals. The bacteria were added to autoclaved faecal pellets and offered to male, subadult specimens of *Oniscus asellus* as the single food source.

Only those faeces-bacteria not able to grow on a simple leaf agar were tested in the feeding experiment. These species were regarded as special inhabitants of the faeces and possibly involved in the phenomenon of coprophagy.

Small amounts of mucous bacterial mass were taken up from the agar plates, suspended in 2 ml physiological NaCl-solution, and added to 0.4–0.6 g autoclaved faeces from *Oniscus asellus*. Eight combinations, each consisting of two bacterial strains, and one combination using all ten tested strains were offered to groups of *Oniscus*

Fig. 1. Multiflagellated pseudomonad from partly-decayed leaf litter. fl = flagella. 14,250×

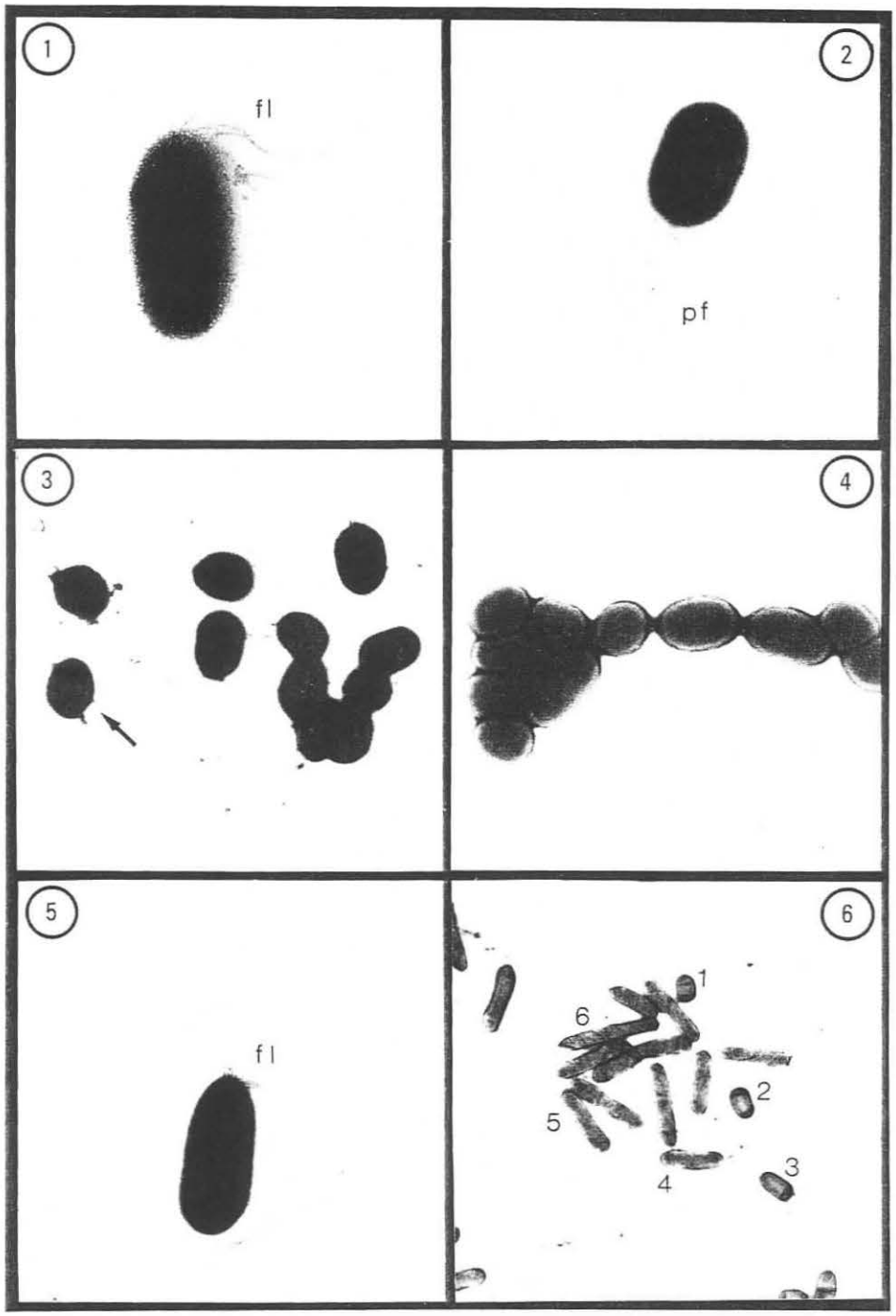
Fig. 2. *Acinetobacter calcoaceticus* with polar fimbriae (pf) from leaf litter. 14,250×.

Fig. 3. Gram negative strain isolated from the midgut glands with a striking subpolar flagellum (arrow = insertion of the flagellum). 10,200×.

Fig. 4. Agglutinated cells of the genus *Arthrobacter* isolated from faeces. 14,250×.

Fig. 5. Monopolar flagellated pseudomonad living on the faeces of *Oniscus asellus*. 14,250×.

Fig. 6. Strain from the faeces with a rod-coccus cycle. 1–6: stages connecting coccus and rod. 7,125×.


1
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asellus, each 7 individuals large, where the individuals of each group were kept isolated in small chambers (1.5 cm·1.5 cm·2 cm) drilled into a gypsum plate. The bottom of the chamber-plate was sealed by a plastic mesh (mesh size 1.5 mm) so that the woodlice had no access to their own faeces. A first control group, also of 7 *Oniscus asellus*, were fed only autoclaved faeces; the faeces for a second control were supplemented with shredded carrots.

Food was changed two times a week to prevent a fungal and bacterial reinfection. The experiment was carried out at 14 °C. Changes in body mass were determined with an accuracy of ± 0.01 mg.

3. Results

3.1. Leaf litter bacteria

The majority of the 7 strains isolated from partly-decayed leaf litter belonged to the family Pseudomonadaceae (fig.1). Species of this family are regarded as characteristic members of the primary colonization on leaf litter (CAMPBELL, 1980). None of these strains was able to produce water-soluble pigments.

Furthermore, strains belonging to *Acinetobacter calcoaceticus alcaligenes* and *A. c. anitratus* were detected. These common soil- and water-dwelling bacteria are characterized by polar fimbriae (fig. 2). Spore forming rods were represented by *Bacillus cereus var. mycoides*, a form easy to identify because of its fungus-like growth on solid nutrient agar.

3.2. Bacteria in the intestinal tract of *Oniscus asellus*

Seven representatives of 4 different bacterial families could be isolated from the intestine of the three starved specimens.

The stomach showed only two plateable strains of bacteria, which belonged to the families Corynebacteriaceae and Pseudomonadaceae. The member of the Corynebacteriaceae exhibited complex nutritional needs and was not able to grow in a medium containing only a peptone. Plateable strains of bacteria inhabiting the midgut glands could only be found in one specimen of the three used for isolation. The gram negative strain obtained possessed a coccoid to short rod shape with a single subpolar inserted flagellum (fig. 3) and was able to grow anaerobically. A negative oxidase test, the formation of gas from glucose, and the positive methyl-red test indicated affinities to the Enterobacteriaceae.

Among the resident members of hindgut-bacteria, the coryneform species formed the largest group. Three of four isolated strains were identified as members of this group. Besides small *Arthrobacter*-like, coccoid forms, typical drum-stick shaped pleomorphic rods also occurred. Another bacterial strain from the hindgut also exhibited a coccoid shape with clusters of cells on light microscopic observations and produced smooth white colonies on TYA. This strain, belonging to the family Micrococcaceae, probably represents a common saprophytic from.

3.3. Faeces-Bacteria

The faeces of *Oniscus asellus* as "biochoria" (SUDHAUS, 1981) in the leaf litter showed a dense and rich bacterial population. By aerobic incubation on TYA, 17 different strains could be isolated.

The dominant bacteria in the gut and on the faeces belonged to the same group. Similar results were obtained in the woodlouse *Tracheoniscus rathkei* [REYES & TIEDJE, 1976].

In *Oniscus asellus*, members of this group, the coryneform bacteria, could not be found on the decayed leaves. Among the 12 coryneform strains (about 70% of all strains isolated), three produced a striking orange pigment. Whereas two of them were identifiable through their club-shaped appearance and their small filamentous rods (max. 12 µm) as Corynebacteriaceae, the third appeared significantly pleomorphic with cocci of 1 µm to long (20–30 µm) and branched filaments, which showed a characteristic banded appearance following Gram-staining. This species could be placed in the Mycobacteriaceae, which are closely related to the Corynebacteria-

ceae. One isolate, unable to produce acid from sugars and showing a rod-coccus cycle, was identified as a species of the genus *Arthrobacter* (fig. 4). Only a single strain of the Corynebacteriaceae, producing small cocci (ca. 0.5 µm) in older cultures, showed the ability to grow also under anaerobic conditions.

The family Pseudomonadaceae, represented on the faeces by three species of the genus *Pseudomonas*, formed only ca. 18% of all isolated strains. Apart from regular rod-shaped strains (fig. 5), one isolate developed long rods extending up to 12 µm, the six-fold length of "regular" rods. This phenomenon is known from plant-pathogenic species (KRIEG & HOLT, 1984).

A further isolated strain, *Chromobacterium violaceum*, with its characteristic blue-purple appearance on TYA, represents a potentially human pathogenic form widespread in soil and water (FINEGOLD & BARON, 1986). One strain, exhibiting a subpolarly inserted single flagellum in coccoid forms and connected with longer rods by transitional stages (fig. 6), could not be determined definitely.

Seven out of seventeen strains of faeces-bacteria were able to grow on leaf agar. An interesting exception were the striking orange and yellow coloured coryneform bacteria, whose nutritional needs could not be satisfied by the leaf agar. Their culture was only possible on a rich TYA medium.

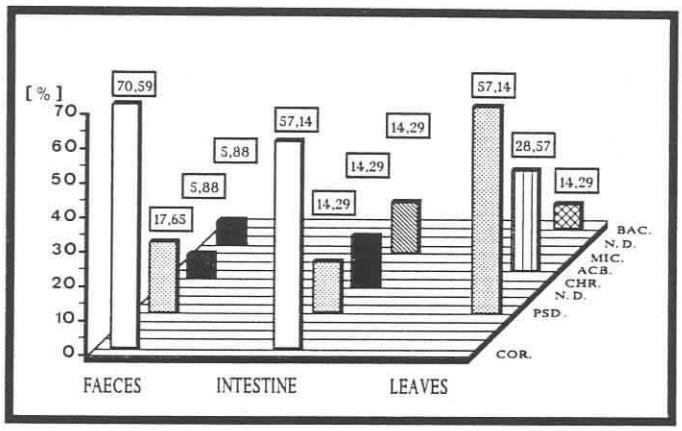


Fig. 7. Composition of the bacterial microflora on faeces, intestine, and leaves. COR. = coryneform bacteria, PSD. = pseudomonads, N. D. = not determined, CHR. = *Chromobacterium violaceum*, ACB. = *Acinetobacter calcoaceticus*, MIC. = Micrococcaceae, BAC. = *Bacillus cereus*.

Members of the family Spirillaceae, which were only discovered in liquid trypton-yeast medium, did not possess the ability to grow under a normal air oxygen content on a solid medium.

The percentage of different bacterial strains of the platable microflora on faeces, intestine, and leaves is given in fig. 7.

3.4. Refeeding of Faeces-Bacteria

The feeding of faeces-bacteria to *Oniscus asellus* offered autoclaved faeces showed the different nutritional quality of the tested strains and their various importance in supplementing the natural diet of the woodlice.

The addition of living bacteria to the faeces generally resulted in an increased survival rate of the animals compared to those fed on pure sterilized faeces (fig. 8). Very successful in keeping the animals alive was the combination of 10 faeces-bacteria. Only one animal died after 103 days and then only because it was hurt during handling. Despite the nearly identical survival rates between the feeding experiments with faeces with 10 bacterial strains (fig. 9) and faeces supplemented

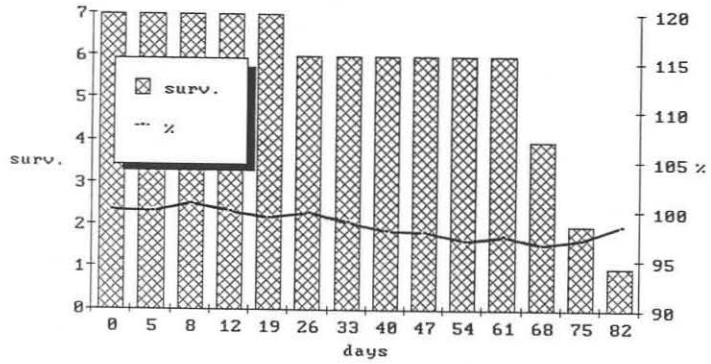
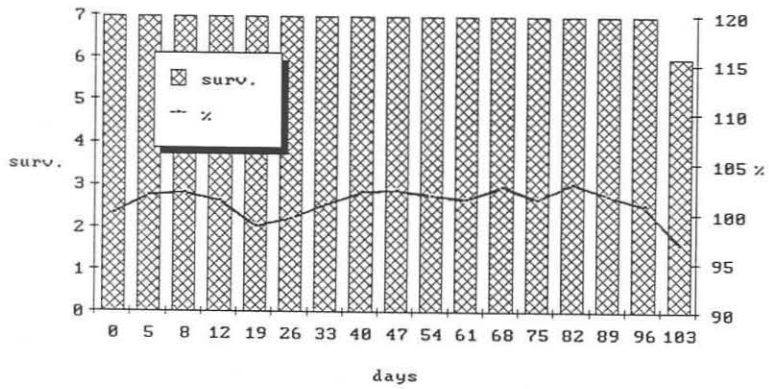


Figure 8



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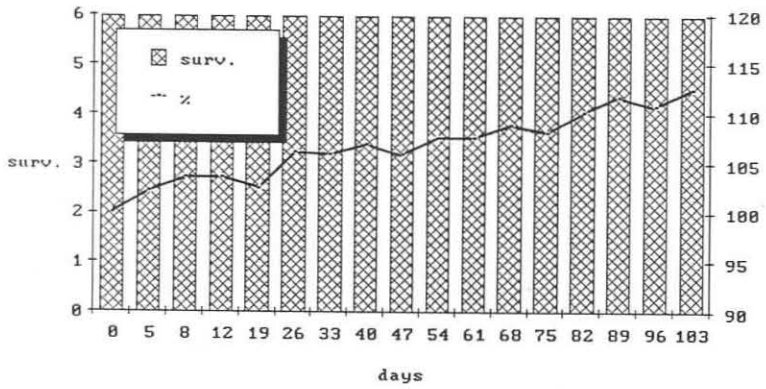

Figure 10

Figs. 8–12. Survival rates and changes in body mass of specimens of *Oniscus asellus* fed sterilized faeces alone (8) or supplemented with 10 strains of isolated faeces bacteria (9), shredded carrots (10) or 2 isolated strains of faeces bacteria (11, 12). surv. = number of living animals, % = changes in body mass on the base of initial mass (= 100 %).

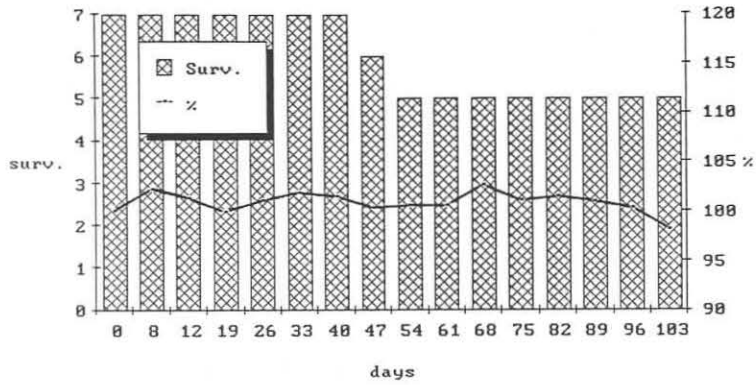

Figure 11

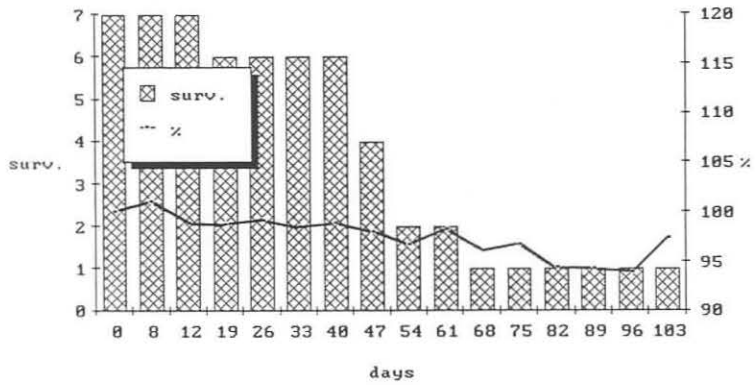

Figure 12

with shredded carrot (fig. 10), a remarkable difference in the development of the average body mass existed between the two groups.

At day 103, the specimens fed with faeces and carrots had reached an average weight of 112.42 ± 7.38% (starting mass = 100%, see fig. 10). The 10 bacterial strains on the faeces fed the other group appeared to permit no increase in body mass (animals with an average mass of 96.83 ± 9.19%, see (fig. 9).

The other groups, receiving a combination of only two bacterial species on their feeding substrate, reached on the one hand survival rates nearly as good as the group fed with 10 bacterial strains (see fig. 11), although on the other hand hardly better than those fed only pure faeces (fig. 12). In both cases, members of the coryneform bacteria were used as food.

4. Discussion

Microorganisms play an important role in the life of woodlice. By acquiring enzymes such as cellulases from ingested bacteria (HARTENSTEIN, 1964), or by receiving supplements to a deficient artificial diet (CAREFOOT, 1984a; CAREFOOT, 1984b), woodlice benefit extensively from the abilities of bacteria.

In order to assess the shift in bacterial strains while passing the intestinal tract of *Oniscus asellus*, the leaf inhabiting bacteria were determined. In contrast to the intestinal tract and the faeces, no member of the coryneform bacteria could be isolated from the partly decomposed leaves. This effect may be due to the abilities of some Pseudomonadaceae to produce growth-inhibiting substances, which act against *Arthrobacter*-species, belonging to the Corynebacteria-

ceae [SIEBURTH, 1967; CHAN & KATZNELSON, 1961]. The determined dominance of the pseudomonads on fallen leaves agrees with the results of INESON & ANDERSON (1985).

After being taken up with the leaves, the fate of the adhering bacteria is quite different. To distinguish beween bacteria being digested and assimilated by the woodlouse and such forms possessing the ability to resist complete digestion in the intestinal tract and forming more or less stable populations and representing resident members of a specific gut flora, only starved animals were examined. In starved specimens, regardless if vertebrates (SAVAGE, 1977) or woodlice (REYES & TIEDJE, 1976), the bacterial counts in the gut drop sharply. The remnant strains in *Oniscus asellus*, the majority of which are members of the Corynebacteriaceae, are resistant to gut passage or benefit from it. These gram positive bacteria are known as regular inhabitants of crustacean digestive tracts, e.g. for the krill *Euphausia superba* [KELLY *et al.*, 1978] and the decapod *Penaeus japonicus* [YASUDA & KITAO, 1980], but they were also found in the gut of the millipede *Schizophyllum sabulosum* [INESON & ANDERSON, 1985]. The unidentified bacteria observed by WOOD & GRIFFITHS (1988) in the midgut glands of *Oniscus asellus* with a rod-like to filamentous form and a gram positive staining can probably be attributed to the coryneform bacteria.

The isolated species of Pseudomonadaceae and Micrococcaceae, however, possibly represent only common, saprophytic soil dwelling forms. The same may be so for Enterobacteriaceae and Vibrionaceae, identified by GRIFFITHS & WOOD (1985) in the hindgut of *Oniscus asellus*. In contrast to these taxa, the coryneform bacteria, which persist in the intestine for a certain time, may auxiliant for the woodlouse in a special way.

A comparison with the results of INESON & ANDERSON (1985) for the gut flora in *Tracheoniscus rathkei*, which were fed continuously, showed that after starvation most of the gram negative bacteria able to grow anaerobically disappeared. Gram positive bacteria survived longer, which may possibly represent a specific intestinal microflora of *Oniscus asellus*. This shift from gram negative bacteria (dominating on the food) to gram positive forms (as prominent inhabitants of the gut in starved animals) also corresponds with the results of GUNNARSSON & TUNLID (1986), by measuring the content of diaminopimelin acid and other characteristic bacterial components, they determined an increase in the relative amount of gram positive bacteria on aging faeces.

On the faeces and in the intestinal tract of *Oniscus asellus*, this shift seems first of all to be based on an increase of the coryneform bacteria.

The faeces of animals go through different stages of a succession before reaching a final humification. After the dismission of the faecal pellets, the colonization with environmental microorganisms starts. Whereas in *Tracheoniscus rathkei* only 22% of the gut species were able to grow on a leaf agar [REYES & TIEDJE, 1976], 40% of the plateable strains from *Oniscus asellus* faeces showed this ability, indicating an increasing colonization by litter microorganisms.

The 2–3 week old faeces of *Oniscus asellus* form an ideal substrate, especially for the coryneform bacteria, which are the dominant members of the coprophilous microflora. Faecal pellets of this age were preferentially ingested by the coprophagous *Oniscus asellus* [HASSALL & RUSHTON, 1985]. The nutritional value of bacterial ingested with different substrates like faeces or natural food stuff for isopods or other arthropods is quite different.

In short-term feeding experiments, providing different species of terrestrial isopods pure cultures of *Bacillus subtilis*, *Escherichia coli* and *Bacillus thuringiensis*, STORCH (1984) described the ultrastructure of the large cells in the midgut glands, which represent sensible indicators for the actual nutritional condition of the animal. The ultrastructural features of these cells after bacterial feeding showed the good quality of this food. Further experiments with *Ligia italica* [ŠTRUS *et al.*, 1985] yielded similar results.

In contrast to these findings, feeding with bacteria as a basic food permits in the long run no mentionable increase in body mass. Different rates of mortality in the tested woodlice indicated the different value of the ingested bacteria in the nutrition of *Oniscus asellus*. The same is also true for the isopod *Asellus aquaticus* [WILLOUGHBY & MARCUS, 1979] or other Crustacea such as *Artemia salina* [YASUDA & NOBUO, 1980].

The total contribution of bacterial biomass ingested with faeces and natural food to the energy requirements for *Oniscus asellus* must be estimated as very low. Further references for this

opinion can be found in the publication of FINDLAY *et al.* (1984) on the freshwater isopod *Lirceus spec.* and BAKER & BRADNAM (1976) on the role of bacteria adhering to the natural food stuff in the nutrition of aquatic larvae of Diptera and Ephemeroptera. The authors concluded that the quantitative contribution of ingested bacterial biomass seems negligible, however regarding its quality (e.g. vitamins, enzymes, amino acids) it may be very important for the animal. The purpose of the coprophagous behaviour in terrestrial woodlice can probably be attributed to this.

For a period of 2–3 weeks after ejection, faecal pellets form an ideal substrate for bacteria (HASSALL *et al.*, 1987; LODHA, 1974). These high bacterial densities are associated with the presence of easily assimilatable carbohydrates (NICHOLSON *et al.*, 1966) and other substances, a suitable *p*H (HANLON, 1981), and a dispersed physical structure (LODHA, 1974), all responsible for the good growth of these in majority aerobic faeces bacteria. The noticed dominance of the coryneform bacteria in the gut and on the faeces of *Oniscus asellus* indicates the suitability of these environments for the coryneforms. Thus this group of bacteria (together with other gram positive forms) is one of the major suppliers of extracellular enzymes (PRAMER, 1968) and essential amino acids (CRUEGER & CRUEGER, 1982).

The woodlouse *Oniscus asellus* uses its faeces as a culture medium for environmental bacteria and "harvests" them after a dense and diverse microbial population has been established. Their role for the woodlouse may be that of "microbial auxiliaries", assisting by disintegration of the natural food source by releasing e.g. phenolic-bound vegetable proteins (KAPLAN & HARTENSTEIN, 1978; HAIDER *et al.*, 1965) and supplementing it with trace nutrients such as essential amino acids. These may be the major benefits of ingesting the faecal microflora.

Changes in the environment of the woodlouse, such as contamination of the soil with toxic xenobiotics or the effects of acidification, which disturb the microbial communities, may also directly and indirectly influence the woodlice. By inhibiting or eliminating possibly auxiliant microorganisms, long-term negative effects on woodlice cannot be excluded. As one of the important macro-decomposers in temperate regions, whose diverse activities enhance decomposition in soil (GRÜNWALD, 1988, GRIFFITHS *et al.*, 1989), consequences in decomposition rates and nutrient cycling in the soil would follow.

5. Acknowledgements

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Synopsis: *Original scientific paper*

ULLRICH, B., V. STORCH, & H. U. SCHAIRER, 1991. Bacteria on the food, in the intestine and on the faeces of the woodlouse *Oniscus asellus* (Crustacea, Isopoda): Species composition and nutritive value. Pedobiologia **35**, 41–51.

The species composition of the bacterial microflora on partly decomposed leaves, in the intestinal tract of *Oniscus asellus* starved for 12 days, and on the 2–3 week old faecal pellets from *Oniscus asellus* was determined. The dominating elements in the intestine and on the faeces were the coryneform bacteria in contrast to the leaves, where pseudomonads formed the major group. These bacteria, known as suppliers of extracellular enzymes and essential amino acids, seem to be involved in coprophagy.

Feeding experiments with pure cultures of faeces bacteria, added to autoclaved faecal pellets of *Oniscus asellus*, showed that the bacterial biomass growing on faeces contributes only a negligible quantity to the energy requirements of the woodlouse. The different nutritive values of the special faeces-inhabiting bacteria became evident.

Key words: Bacteria, faeces, intestinal tract, coprophagy, nutrition, *Oniscus asellus*.

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